

Effects of Flow Speed on Growth of Benthic Suspension Feeders

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Abstract. In separate experiments in 1991 and 1992, the sensitivities of growth rates of six species of benthic suspension feeder to flow speed were tested in a series of turbulent pipe flows. Species examined were the cheilostome bryozoan *Membranipora membranacea* (1991); the serpulid polychaete *Pseudochitinopoma occidentalis* (1991); and the barnacles *Balanus glandula* (1991), *B. crenatus* (1992), *Semibalanus cariosus* (1992), and *Pollicipes polymerus* (1992). In both experiments, animals were exposed to one of five constant, narrow ranges of speed that varied from about 2–15 cm s⁻¹. Growth rates of *Membranipora* and *Pseudochitinopoma* in 1991 declined significantly and monotonically with increasing flow speed, despite evidence that at faster flows there were greater concentrations of suspended food available and higher particulate fluxes. In contrast, there was no detectable relationship between speed and growth of *B. glandula* over the same range of flow speeds in 1991. Results of the 1992 experiment indicated variability in growth responses among three species of barnacle. Growth rates of *S. cariosus* and *P. polymerus* were insensitive to flow speed, whereas growth rates of *B. crenatus* increased from low speeds to a maximum at an intermediate speed of about 8 cm s⁻¹, and then tended to decrease at higher speeds. Combined results of the two experiments indicate that the growth response of animals to flow was most obviously related to the relative flow energy of the animal's natural habitat. Growth rates of animals that typically experience relatively weak flows (*P. occidentalis*, *M. membranacea*, and *B. crenatus*) were affected significantly by flow speed, whereas growth rates of animals from comparatively high-energy environments (*B. glan-*

dula, *S. cariosus*, and *P. polymerus*) were relatively insensitive to flow speed. In contrast, animal morphology and behavior were not obviously related to growth responses to flow. A key to understanding the impact of flow on a suspension-feeder's growth may be the animal's ability to handle and process particles that have impacted the feeding apparatus and to deliver them to the point of ingestion.

Introduction

One clear trend that has emerged from many studies of effects of flow speed on both passive and active suspension feeders is that rates of particle capture or growth are lower on both sides of a narrow range of intermediate speeds that appear to be most beneficial. This pattern has been demonstrated for growth of a scallop (Kirby-Smith, 1972) and particle capture by an alcyonacean coral (McFadden, 1986), a sea pen (Best, 1988), a crinoid (Leonard *et al.*, 1988), and a gorgonian coral (Sponaugle and LaBarbera, 1991). There are several causes for this trend. As flow speed increases from near-zero levels, rates of particle encounter with passively deployed filter elements increase (Shimeta and Jumars, 1991), and increased turbulent mixing makes depletion of food particles within the animal's feeding ambit less likely (Wildish and Kristmanson, 1979; Patterson, 1984; Fréchette and Bourget, 1985; Fréchette *et al.*, 1989). At relatively high flow speeds, deformation of filtering structures may reduce the total surface area available for particle capture (Patterson, 1984; Harvell and LaBarbera, 1985; Best, 1988; Shimeta and Jumars, 1991), particles impacting filter elements may be handled or processed with greatly reduced efficiency due to drag effects (Patterson, 1991; Shimeta and Jumars, 1991), or adverse pressure gradients may inhibit process-

ing of water containing suspended particulate food (Wildish *et al.*, 1987).

The trend of maximum particle capture or growth at intermediate flow speeds has not been exhibited in all studies that have addressed the relationship, however. By restricting study to a comparatively narrow range of flow speed on either side of the intermediate speed of maximum growth (nearly always unknown *a priori*), a simpler direct or inverse relationship between speed and particle capture or growth would appear. Thus, a monotonic increase in particle capture with flow speed was noted for a coral (Sebens and Johnson, 1991), but inverse relationships were reported between flow speed and scallop growth (Wildish *et al.*, 1987; Eckman *et al.*, 1989; Wildish and Saulnier, 1992), barnacle growth (Smith, 1946), and particle capture or growth by bryozoans (Okamura, 1984, 1985, 1992).

Despite the attention devoted to this topic of research, some important gaps remain in our understanding of the influence of flow on growth of suspension feeders. First, because prior studies have focused on individual species, it is not yet clear how different species, which have different behaviors and employ different mechanisms of suspension feeding, will respond to the same range of conditions. This knowledge would be useful in determining how assemblages of suspension feeders might become partitioned in space according to flow microhabitat, or in predicting the relative competitive success among species that exhibit differential sensitivities to flow. The relative competitive abilities of suspension-feeding species may well vary among sites depending on their flow energies. Second, for tentaculate suspension feeders (*e.g.*, hydrozoans, bryozoans, gorgonians), there is little evidence that the relationship between flow speed and particle capture (the dependent variable typically evaluated for this diverse guild) translates into identical effects on growth. This result may seem logical, but it has been demonstrated only by Okamura (1992). Moreover, the translation of particle capture to growth may not always be straightforward. For example, for two bryozoans there was a change in direction of the dependence of particle capture rate on flow speed as food-particle size changed over a comparatively narrow range (Okamura, 1987). Consequently, for tentaculate suspension feeders that enjoy a comparatively diverse diet, relationships between flow speed and capture rates of one particle type may not translate faithfully into growth responses.

We therefore carried out two experiments testing effects of flow speed on growth rates of several species of sessile, benthic suspension feeder. Our first experiment, carried out in 1991, involved the cheilostome bryozoan *Membranipora membranacea*, the barnacle *Balanus glandula*, and the serpulid polychaete *Pseudochitinopoma occiden-*

tal. These species all feed via a structure that is extended into the flow, beyond the calcareous zoecium, test, or tube that encloses the main body of the colony or animal. However, the behavior and the mechanism for operation of the feeding organ vary among these species, which may affect their relative growth responses to flow. In the first experiment, only the barnacle grew at rates independent of flow speed. Based on this result, we conducted a second experiment in 1992 to determine whether other barnacles from a wide range of habitats showed growth responses similar to that observed in *B. glandula*. This experiment involved the balanoids *B. crenatus* and *Semibalanus cariosus* and the pedunculate species *Pollicipes polymerus*. Finally, to complement these experiments, we also examined the feeding behavior of most of these species as a function of flow speed.

Materials and Methods

Experiments were conducted at the Friday Harbor Laboratories of the University of Washington. In both experiments, effects of flow speed on growth were determined using animals suspended in pipes characterized by steady, turbulent flows. Relationships describing turbulent flow through a pipe are well known (*e.g.*, Schlichting, 1979; Vogel, 1981), making it comparatively simple to establish, monitor, and describe flow velocities to which animals were exposed.

Experimental apparatus—1991

Five narrow ranges of flow speed were established within 10 PVC pipes (two replicates per speed). Each pipe was 3-m long and either 2.5 cm or 3.8 cm in radius. All pipes were submerged in a seawater bath within a single tank that was 3.66-m long, 1.22-m wide, and 1.22-m deep. Pipes were aligned in parallel in a single row along the bottom of the tank, and were assigned randomly to different flow speeds. The pipes passed through a water-tight partition inside the tank, 1.22 m from one end. A diaphragm pump continuously supplied the smaller compartment of the tank (the head) with fresh seawater from a depth of 4 m. An overflow pipe in the head tank kept the seawater at a constant depth. The high rate of discharge of the pump (about 31 s^{-1}) mixed water in the head tank thoroughly. An overflow pipe in the other section of the tank (the tail) kept seawater at a constant, lower depth. The resulting constant pressure gradient between the head and tail ends drove steady flows through the pipes. The rate of flow through each pipe was regulated with an adjustable valve located at the discharge end of each pipe.

Six windows (each about $2.5 \times 4 \text{ cm}$) were cut in the wall of each pipe through which were inserted thin strips of plexiglass containing animals used in growth studies

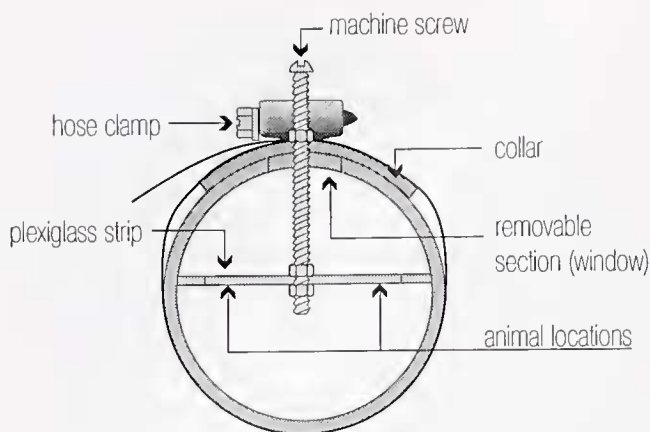


Figure 1. Cross-sectional view of the apparatus used to position suspension feeders within pipe flows. The hose clamp created a nearly watertight seal between the cut-out section of pipe mounted on the collar and the main body of the pipe.

(Fig. 1). The first window was cut 110 cm downstream of the pipe's entrance, and the other five windows were spaced 20-cm apart. The remaining downstream section of each pipe was used in a larval settlement study that will be described elsewhere. Each cut-out section of pipe was glued onto a larger PVC collar that could be clamped onto the pipe to make a nearly watertight seal. This entire assembly was removable. A machine screw passed through a hole in the collar and the section of pipe from which the window was cut (Fig. 1). The screw was used to suspend plexiglass strips containing animals across the diameter of each pipe. Plexiglass strips were 0.16-cm thick, spanning 2 cm in the along-stream dimension and either 5 or 7.6 cm across-stream, depending on the pipe's diameter. Strips were mounted level within pipes (*i.e.*, normal to gravity) such that all animals were facing down.

The growth experiment ran from 6 June–22 November 1991. During this period discharge rates of the pipes (Q) were measured on 17 separate dates. Pertinent characteristics of turbulent pipe flows were calculated from pipe discharge rate and radius (R) using relationships either given by Schlichting (1979) and Vogel (1981) or derived from equations they presented. The mean flow speed within each pipe (U) was

$$U = Q/(\pi R^2) \quad (1)$$

Pipe Reynolds number (Re) was

$$Re = U(2R)/\nu \quad (2)$$

where ν is the kinematic viscosity of seawater ($0.01 \text{ cm}^2 \text{ s}^{-1}$). The flow speed (U_y) at any distance y from the pipe's wall ($y = 0$) was

$$U_y = U_{\max}(y/R)^{1/n} \quad (3)$$

where U_{\max} is the maximum flow speed (along the pipe's center line) and

$$n = 6 + 0.6((Re - 4000)/19,000) \quad (4)$$

Eq. (4) was derived from Eq. (20.6) and Fig. (20.3) in Schlichting (1979, p. 599). From Eqs. (3, 4) one can calculate the maximum and minimum (U_{\min}) speeds to which feeding organs of animals in any pipe were exposed, assuming that they were a distance at least 10% of the radius away from the pipe wall:

$$U_{\max} = U(1 + 1/n) \quad (5)$$

$$U_{\min} = U_{\max}(0.1)^{1/n} \quad (6)$$

As seawater entered the pipe from the head tank, a boundary layer developed along the pipe's wall. Eqs. (3–6) are valid only for a fully developed flow, which existed at all locations downstream of the distance (X_{eq}) required for the boundary layer to grow to a thickness equal to the pipe's radius. For a turbulent boundary layer, this distance was approximately

$$X_{\text{eq}} = (R/0.37)^{1.25}(U_{\max}/\nu)^{0.25} \quad (7)$$

as derived from Schlichting (1979, his Eq. 21.8).

Table 1 lists flow properties for each of the 10 pipes in the experiment, based on the mean of the 17 separate measurements of discharge rate. In all cases, flow was fully developed before the first animal was encountered 110-cm downstream of each pipe's entrance (*i.e.*, $X_{\text{eq}} < 110 \text{ cm}$). There were five levels of mean speed (U) that ranged from about 2–15 cm s^{-1} . Within each pipe there was little temporal variability throughout the experiment (Table 1); the coefficient of variation (standard deviation/mean) of U averaged 6.45%. However, due to the radial velocity gradient (Eq. 3), the range of flow speeds experienced by animals within a pipe could have been as great as $\pm 10\%$ – 15% of U .

It is important to note that a boundary layer also developed along each plexiglass strip to which animals were attached. Calculations (based on Eq. 21.8 in Schlichting [1979]) indicate that this boundary layer could have been no more than a few millimeters thick, even at the downstream end of each 2-cm-long strip, given the flow velocities in Table 1. Because the feeding structures of animals studied extended even greater distances above the substratum (Eckman and Duggins, 1991; personal observations), the effect of this boundary layer on flow speeds experienced by animals can be ignored, and animals were exposed to speeds reported in Table 1.

Experimental protocols—1991

Colonies of *Membranipora membranacea* were obtained after larvae settled onto large strips of plexiglass

Table 1

Average properties of pipe flows, arranged in order of increasing mean flow speed, in the 1991 and 1992 experiments

Pipe No.	R (cm)	Q (cm ³ s ⁻¹)	Re	U (cm s ⁻¹)	U_{max} (cm s ⁻¹)	U_{min} (cm s ⁻¹)	X_{eq} (cm)
1991 Experiment							
7	3.8	85.7	1433	1.9 (.04)	2.2	1.5	71
1	3.8	93.8	1567	2.1 (.03)	2.4	1.6	73
8	2.5	84.8	2124	4.2 (.11)	4.9	3.3	52
3	2.5	92.5	2317	4.6 (.22)	5.3	3.6	53
10	2.5	141	3527	6.9 (.24)	8.1	5.5	59
4	2.5	142	3555	7.0 (.17)	8.2	5.6	59
5	2.5	227	5692	11.2 (.31)	13.0	8.9	67
9	2.5	228	5706	11.2 (.30)	13.1	8.9	67
2	2.5	297	7446	14.7 (.30)	17.1	11.7	71
6	2.5	299	7482	14.7 (.35)	17.1	11.8	71
1992 Experiment							
5	5.1	—	2652	2.6	3.0 (.12)	2.3	111
10	5.1	—	2805	2.8	3.2 (.10)	2.4	112
9	5.1	—	5457	5.4	6.2 (.10)	4.8	133
4	5.1	—	5457	5.4	6.2 (.10)	4.8	133
3	5.1	—	8160	8.0	9.2 (.10)	7.2	147
8	5.1	—	8160	8.0	9.2 (.06)	7.2	147
2	5.1	—	10812	10.6	12.3 (.06)	9.5	157
7	5.1	—	10914	10.7	12.4 (.15)	9.6	157
6	5.1	—	13158	12.9	14.9 (.29)	11.6	165
1	5.1	—	13464	13.2	15.3 (.05)	11.8	166

Pipe No. refers to the relative position of pipes in the tank. R is inner radius. Q is discharge rate (not measured in the 1992 experiment). Re is Reynolds number. U , U_{max} and U_{min} refer, respectively, to mean flow speed, maximum speed along the centerline, and minimum speed experienced by animals. Standard error (in parentheses) is given for U in the 1991 experiment and U_{max} in the 1992 experiment. X_{eq} is the distance downstream from the entrance required to achieve fully developed flow.

attached to racks suspended at a depth of about 2 m. Strips for deployment in pipes were cut from these larger strips such that each contained two or more colonies < 2 mm in diameter. Colonies on strips were photographed, using a video camera, just before they were placed in pipes on 6 June. Strips were removed from pipes on 25 June, and colonies were rephotographed.

Colonies that had grown to contact other colonies were not analyzed because intraspecific contact interferes with growth (Ellison and Harvell, 1989). Although most of the remaining colonies were circular on 25 June, many others contained invaginations, probably as a result of partial predation (Harvell *et al.*, 1990) inflicted by gastropods introduced into pipes by the pump. To minimize effects of these invaginations on estimates of growth, a "potential growth rate" of each colony was calculated as in Eckman and Duggins (1991). Potential growth was defined as the difference in areas of circles with radii equal to the maximum radius of each living colony (*i.e.*, the farthest distance from ancestrula to colony edge) on 6 and 25 June. Maximum radii were estimated from photographs made on 6 June and measured directly using calipers on 25 June. Use of this method, rather than simple differences in total colony area, allowed us to minimize the influence

of factors such as predation, which would have reduced the size of the colony only at certain points along its edge. Use of this method is further justified since estimates of potential growth rate are strongly correlated with absolute measures of growth rate based on increase in colony area (see Results).

One assumption implicit in the use of this method is that colony growth was isotropic, and not sensitive to flow direction in pipes. To evaluate this assumption quantitatively, we measured maximum dimensions (on 25 June) of 45 haphazardly selected colonies in both across-stream and along-stream directions. The ratio of these dimensions should be 1.0 if growth was insensitive to flow direction.

Balanus glandula was obtained after cyprids settled onto large strips of plexiglass attached to rocks in the lower intertidal. Strips for deployment in pipes were cut from these larger strips such that each contained two or more small individuals. Animals on strips were photographed just before being placed in pipes on 1 August. At that time the mean basal diameter of all barnacles was 14.3 mm²; the range was 5–31 mm². Strips were removed from pipes on 24 September, and animals were rephotographed. Growth was defined as the increase in basal area of animals

still alive on 24 September. Barnacles that had grown against neighbors were not considered.

Pseudochitinopoma occidentalis was obtained after larvae settled onto large strips of plexiglass attached to racks mounted about 20 cm above the bottom at 10-m depth. Strips for deployment in pipes were cut from these larger strips such that each contained two or more small individuals. Animals on strips were photographed just before being placed in pipes on 26 August. At that time the mean length of the calcareous tube of all individuals was 7.1 mm; the range was 2.5–13 mm. Strips were removed from pipes on 22 November, and animals were rephotographed. Growth was defined as the increase in length of the tube of individuals still alive on 22 November.

By using a small head tank and a pump with a high discharge rate, we hoped to ensure that water supplied to pipes was well mixed and that each pipe received the same initial concentration and composition of suspended particulates as food for suspension feeders. However, the possibility of inhomogeneous supply existed. Moreover, because flows varied in strength among pipes, the rates at which particulates settled out of suspension might have varied among pipes, causing differences in food supply. To assess these effects, we twice sampled seawater that exited each pipe and one time each tested for differences in concentrations of chlorophyll, particulate organic carbon (POC), and particulate organic nitrogen (PON).

For chlorophyll, three replicate samples of 1000 ml were collected from each pipe. One replicate was collected from each of the 10 pipes before collecting the next replicate sample. Each sample was filtered through a 0.22- μm glass-fiber filter. Pigments collected on the filter were extracted in acetone, and chlorophyll was measured spectrophotometrically according to Parsons *et al.* (1984).

The number of replicates and the sampling protocol for POC and PON were the same as for chlorophyll. A subsample of each 500-ml seawater sample (volume varied according to the amount of particulates in the sample) was filtered through a 0.22- μm glass-fiber filter that had been baked at 550°C; all glassware was acid-washed. Filters were immediately dried at 65°C and then frozen. Treatment of the filter to remove carbonates was judged unnecessary because the local phytoplankton and zooplankton assemblages contain few individuals with calcareous tests. Masses of C and N on filters were determined using a Perkin-Elmer 2400 Elemental Analyzer and converted to POC and PON concentrations.

Experimental apparatus—1992

Results of the 1991 experiment prompted us to run a similar experiment in 1992 to evaluate growth responses of three other species of barnacle (*Semibalanus cariosus*,

Balanus crenatus, and *Pollicipes polymerus*) to flow speed. Because our original device had been dismantled, we used a different pipe flow apparatus that had been built for another experiment.

Ten straight sections of pipe were used, as in 1991. Each pipe (5.1-cm inner radius) was 307 cm long. The 10 pipes were submerged in a large, round seawater tank (400 cm in diameter, 55 cm deep) that was supplied continuously with fresh, unfiltered seawater. A standpipe in the tank allowed overflow. All pipes were connected directly to a centrifugal pump that supplied each with seawater (at a constant pressure) drawn directly from the tank in which the pipes were submerged. Flow through each pipe was regulated by a valve at the end of each pipe, as in the 1991 experiment. The connecting pipes that led from the pump to the straight sections used in the experiment also had a 5.1-cm inner radius. These connectors varied in length among the 10 pipes from 20–150 cm. To break down the jet of water that exited the pump, two turns were built into the connectors.

Eight windows were cut in each 307-cm-long straight section of pipe. Animals were introduced into pipes through these windows as in the 1991 experiment (Fig. 1). The first window in each pipe was located 46 cm downstream of the beginning of the straight section. The spacing between windows was 30 cm.

We attempted to duplicate the five flow levels used in the 1991 experiment, again with two replicate pipes assigned to each flow level. Flow speeds were not calculated from pipe discharge (Q) as in 1991, but instead were measured directly using a 2-axis Marsh-McBirney electromagnetic current meter that was placed on the centerline of each pipe through a window 30 cm from the discharge end. Trials that timed injected dye indicated that the walls of the pipe did not interfere with the magnetic field about the probe enough to affect measurements of current speed, and that measurements obtained with the probe were accurate. Speeds measured with the current meter approximated U_{max} , since speed was measured along each pipe's centerline. Other flow parameters were calculated from U_{max} using equations presented above, with one exception. The minimum flow speed to which animals were exposed (U_{min}) was calculated assuming that all individuals were at least 20% of the radius away from the pipe wall (in the 1991 experiment a minimum distance of 10% of R was assumed). This change was justified since barnacles were attached to plexiglass strips by hand in 1992 (see below), and care was taken to place them farther from the pipe wall.

The growth experiment ran from 22 May–30 July 1992. Flows were measured six times during this 69-day period. Table 1 lists flow properties for each of the 10 pipes, based on the mean U_{max} . The coefficient of variation in U_{max}

was <10% for all 10 pipes. Values of X_{eq} in Table I indicate a problem with the experimental apparatus used in 1992. Depending on flow level, two to four of the eight plexiglass strips containing animals were upstream of the minimum distance required to achieve fully developed flow. Animals on these strips (far from the pipe wall) may have experienced flow speeds somewhat slower on average than animals located further downstream. However, calculations indicate that speeds experienced by animals on these upstream strips would have exceeded U_{min} shown in Table I, so the range of speeds between U_{max} and U_{min} is still an accurate indicator of flow speeds experienced by all animals.

Experimental protocols—1992

Small individuals of *Pollicipes polymerus* and *Semibalanus cariosus* were collected from a comparatively high-energy, mid-intertidal zone in the Straits of Juan de Fuca near Clallam Bay, Washington. We collected individuals of both species that had settled onto shells of mussels (*Mytilus edulis* and *M. californianus*), in addition to *P. polymerus* that were attached to plates of larger *S. cariosus*. Relatively small *Balanus crenatus* on discarded aluminum cans were collected from a depth of about 5 m below the public docks of the town of Friday Harbor, Washington. Animals of all three species were returned to the Friday Harbor Laboratories where they were held in seawater tables for several days.

Individuals of all species were glued by hand onto the plexiglass strips that were subsequently placed in pipes. We prepared pieces of mussel shell, aluminum can, or calcareous plate that were about 1 cm² and contained one or two individuals of one of the three species. Two or three pieces of each substrate were attached to each plexiglass strip using a submarine adhesive. We positioned each barnacle such that the extended cirral net would be oriented approximately concave into the flow. In addition, *B. crenatus* and *S. cariosus* can rotate the cirrus into this apparently "preferred" orientation (see below). Species were not segregated among strips, and strips were assigned randomly to pipes. We did not use animals that were in contact with other individuals.

Each animal was measured within 2 days of the start of the experiment. The basal area of each individual of *B. crenatus* or *S. cariosus* was calculated from the average of two orthogonal measurements of basal diameter obtained using calipers. At the start of the experiment, the mean basal diameter of *B. crenatus* was 62.8 mm²; the range was 17.7–130.5 mm². The mean basal diameter of *S. cariosus* was 52.1 mm²; the range was 7.4–139.8 mm². For *P. polymerus* we used calipers to measure the height of the capitulum (distance from the top of the peduncle

to the furthest extension of the plates). At the start of the experiment the mean capitular height was 5.45 mm; the range was 1.6–11.5 mm.

Plexiglass strips were mounted in pipes as in 1991, and animals were exposed to one of the five steady flows from 22 May–30 July. Thereafter, plexiglass strips were returned to seawater tables, and animals were remeasured within several days. Growth is defined as the increase in basal area (*B. crenatus* or *S. cariosus*) or capitular height (*P. polymerus*).

As in the 1991 experiment, pipes were supplied with seawater from a common, presumably well-mixed source so that there would be little variability among pipes in the concentration or composition of suspended particulates supplied to suspension feeders. To assess this variability, on one occasion we sampled the seawater exiting the pipes and tested for differences in concentrations of chlorophyll. Sampling and analytical protocols followed those in the 1991 experiment.

Flume observations—1992

To aid in interpreting results of growth experiments, we observed the feeding behavior of all species (except *Pseudochitinopoma occidentalis*) in a range of flows. Qualitative observations of responses of feeding structures were made in a simple recirculating flume of the type described by Vogel and LaBarbera (1978). The main channel of the flume was 200 cm long and 30 cm wide. A flow depth of about 15 cm was used.

Each species was observed separately. Approximately 20–30 individuals or colonies were placed in the center of the flume approximately midway down the channel. We used barnacles attached to small rocks or aluminum cans to elevate them above the flume's developing bottom boundary layer and to expose them to near free-stream flow speeds. For a similar reason, we cut out small pieces of kelp that were encrusted with colonies of *Membranipora membranacea*, used a cyanoacrylate glue to attach them to strips of plexiglass (≈3 cm × 5 cm × 0.3 cm thick), and suspended them in the free-stream flow.

Each species was observed at four to five levels of flow, with flow held constant for at least 10 min before the observations. For any given speed, no differences in feeding behavior were apparent between accelerating and decelerating flows. Because flow in this crude flume was three-dimensional and not fully developed, we measured horizontal flow speeds as close as possible to the animals being observed. To obtain these measurements we used a Marsh-McBirney current meter and also timed the passage of suspended particulates. We consider measured flow speeds to be only approximations.

Statistical analysis

Regression was used to examine relationships between the mean growth rate of all individuals (or the mean concentration of chlorophyll, POC, or PON) within a pipe and the mean flow speed in the pipe. Mean growth rate was used because individual growth rates within each pipe were not independent, and it would have inflated the degrees of freedom in the regression had individuals been considered separately. The issue addressed by regression, therefore, was whether or not the mean growth rate of a population varied predictably as a function of flow speed.

Prior research on particle capture by suspension feeders suggests that one of two relationships between flow speed and growth would be expected *a priori* (see Introduction): (1) a convex upward relationship in which growth rates are lower on both sides of a narrow range of intermediate speeds that appear to support the highest growth; (2) a monotonically increasing or decreasing relationship. We had no *a priori* reason to expect that any monotonic relationship between growth rate (or concentration) and speed would be linear. Therefore, we searched for a monotonic relationship of the form

$$G = aU^b + c$$

where G is growth rate (or concentration), U is mean velocity, and a , b , and c are constants. We selected constants that produced the maximum r^2 with the constraint that $0.5 \leq b \leq 3$. This range was imposed because higher or lower exponents would in some instances produce strongly curved functions especially sensitive to flow speeds near the end of the range; also, growth rates and concentrations predicted from these functions could have been non-sen-

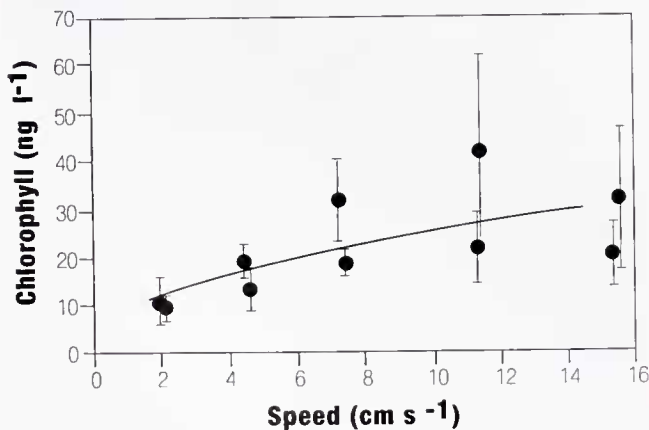


Figure 2. Concentrations of chlorophyll as a function of flow speed measured in each pipe in 1991. Each point and error bar represents the mean (± 1 SE) of three replicate samples obtained from each pipe. Also shown is the best-fit, significant regression line obtained using the 10 mean values.

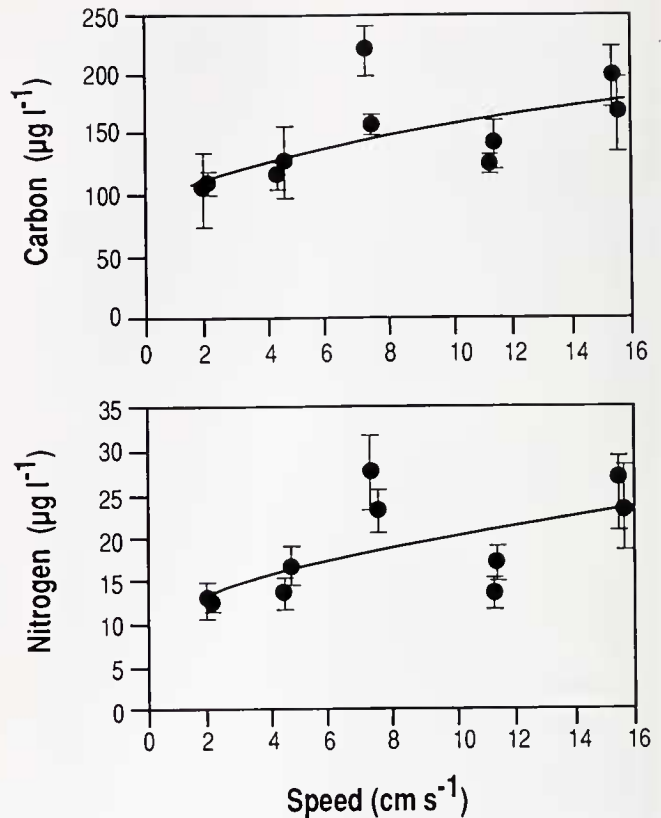


Figure 3. Concentrations of POC (top) and PON (bottom) as a function of flow speed measured in each pipe in 1991. Other interpretations as in Figure 2.

sical (e.g., negative growth of calcareous structures or negative concentrations at near-zero flow speeds).

To evaluate whether growth rate was maximal at some intermediate flow speed, we used a 2nd-degree polynomial to regress growth rate against flow speed:

$$G = aU^2 + bU + c$$

with terms as defined above. A 2nd-degree polynomial defines a parabola, and this functional relationship between growth and speed can assume a convex-upward shape as expected *a priori*.

Results

1991 experiment

The concentration of chlorophyll in pipes increased with flow speed by a factor of more than 2 from 2–15 cm s^{-1} (Fig. 2; $b = 0.5$, $P = 0.03$, $r^2 = 0.46$). The horizontal flux (the product of concentration and velocity) of chlorophyll varied among pipes by a factor of approximately 18 over the 7.5 \times range of flow speeds.

Table II

Numbers of animals per pipe providing measures of growth rate in both experiments

Pipe	1991 Experiment			
	U (cm s ⁻¹)	M.m.	B.g.	P.o.
7	1.9	8	12	12
1	2.1	8	14	14
8	4.2	2	7	6
3	4.6	8	9	5
10	6.9	4	5	2
4	7.0	6	9	5
5	11.2	7	6	2
9	11.2	1	8	6
2	14.7	4	10	6
6	14.7	4	8	7

Pipe	1992 Experiment			
	U (cm s ⁻¹)	S.c.	P.p.	B.c.
5	2.6	7	7	7
10	2.8	3	7	5
9	5.4	7	14	6
4	5.4	6	11	7
3	8.0	7	11	6
8	8.0	3	9	8
2	10.6	6	13	9
7	10.7	6	8	8
6	12.9	4	9	9
1	13.2	6	7	5

M.m., *Membranipora membranacea*; B.g., *Balanus glandula*; P.o., *Pseudochitinopecten occidentalis*; S.c., *Semibalanus cariosus*; P.p., *Pollicipes polymerus*; B.c., *Balanus crenatus*.

Concentrations of POC and PON showed nearly identical patterns (Fig. 3), and resembled the variation in chlorophyll with flow speed. Concentrations of POC and PON both doubled as flow speed increased by 7.5 \times , producing about 15-fold differences in C and N fluxes between the weakest and strongest flows. The regression of POC with speed was significant ($b = 0.5$, $P = 0.05$, $r^2 = 0.39$), and that for PON was nearly significant ($b = 0.5$, $P = 0.06$, $r^2 = 0.38$).

Table II lists numbers of animals of all species from which mean growth rate per pipe was estimated. Growth of *Membranipora* was effectively isotropic at all flow speeds. The ratio of cross-stream to along-stream diameter of colonies was indistinguishable from 1.0 at three of five flow speeds (Table III); diverged slightly from unity, but in different directions, at the other two speeds; and at all speeds was within $\pm 6\%$ of 1.0. Consequently, there was effectively no anisotropic growth that would have biased calculations of potential growth rates. In addition, potential growth rates were strongly correlated with growth rates based on changes in total colony area ($r^2 = 0.81$, $P < 0.0001$, $n = 50$). Potential growth rates of *Membran-*

Table III

Analysis of isotropy in shapes of *Membranipora* colonies

U (cm s ⁻¹)	$D_{\text{xs}}/D_{\text{as}}$	n	P
2	0.967 (± 0.013)	14	*
4	1.010 (± 0.026)	7	NS
7	1.063 (± 0.016)	7	*
11	1.004 (± 0.029)	6	NS
15	0.989 (± 0.023)	11	NS

U is the mean flow speed for each of the five treatments. $D_{\text{xs}}/D_{\text{as}}$ gives the mean ratio (± 1 SE) of colony diameter measured cross-stream to colony diameter measured along-stream. n is the number of colonies. P is the probability that the observed ratio differs from 1.0 (Student's t test); NS = not significant ($P > 0.05$); * = $0.01 < P < 0.05$.

ipora colonies declined monotonically with flow speed (Fig. 4), and the regression was significant ($b = 1.2$, $P = 0.04$, $r^2 = 0.42$).

The large difference in mean colony growth rate between the two replicate pipes at the slowest ("optimal") flow speed (Fig. 4) suggested that conditions in one pipe were anomalously poor. To investigate this possibility we compared probabilities of colony survival among pipes. In both slowest flow pipes, percent colony survival was high (100% and 94%) over the 19-day experiment. The average percent colony survival for all pipes was $84.2\% \pm 11.3\%$ and was not related to flow speed ($r^2 = 0.08$, $P = 0.44$).

Growth rates of *Balanus glandula* individuals were not detectably sensitive to flow speed over the range studied (Fig. 5). There appeared to be a weak (perhaps 10%), but

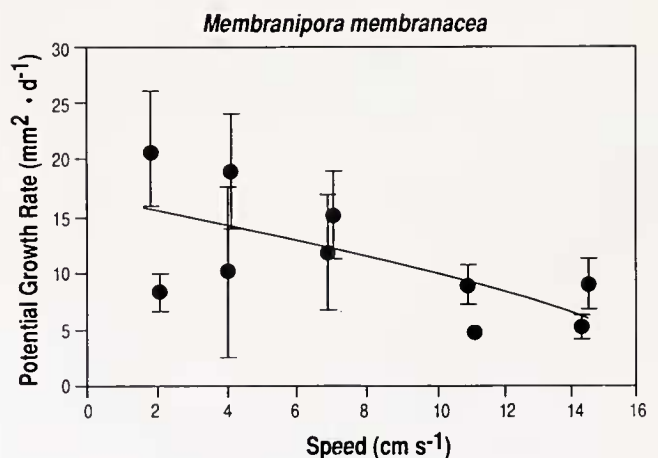


Figure 4. Potential growth rates of *Membranipora membranacea* as a function of the average flow speed measured in each pipe during the 19-day deployment in 1991. Each point and error bar represents the mean growth rate (± 1 SE). Also shown is the best-fit, significant regression line obtained using the 10 mean values.

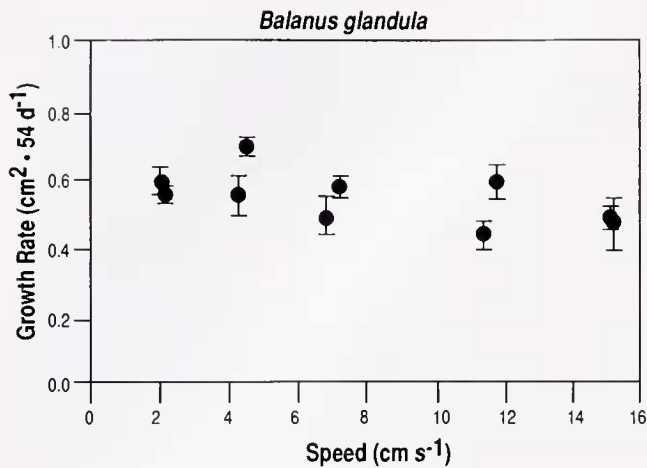


Figure 5. Growth rates of *Balanus glandula* as a function of flow speed during the 54-day deployment in 1991. Other interpretations as in Figure 4. There was no significant best-fit regression.

nonsignificant, monotonic decline in growth rate as speed increased (for all b : minimum $P = 0.10$, maximum $r^2 = 0.30$).

Growth rates of *Pseudochitinopoma* individuals declined monotonically and significantly with flow speed (Fig. 6; $b = 1.1$, $P = 0.009$, $r^2 = 0.59$).

1992 experiment

The concentration of chlorophyll in pipes did not depend on flow speed (Fig. 7). The monotonic regression was not significant (for all b : minimum $P = 0.39$, maximum $r^2 = 0.095$), nor was the polynomial regression.

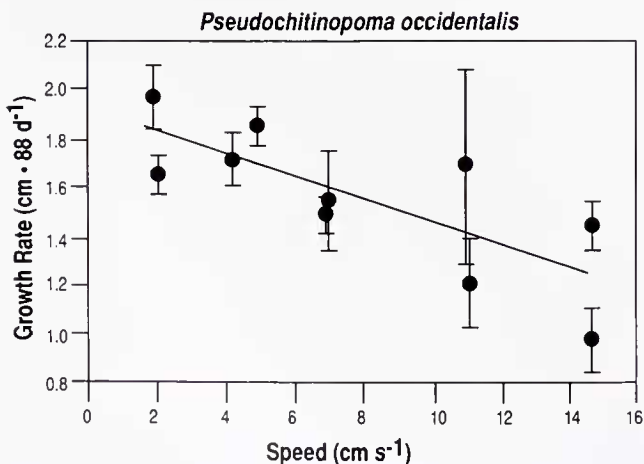


Figure 6. Growth rates of *Pseudochitinopoma occidentalis* as a function of flow speed during the 88-day deployment in 1991. Other interpretations as in Figure 4.

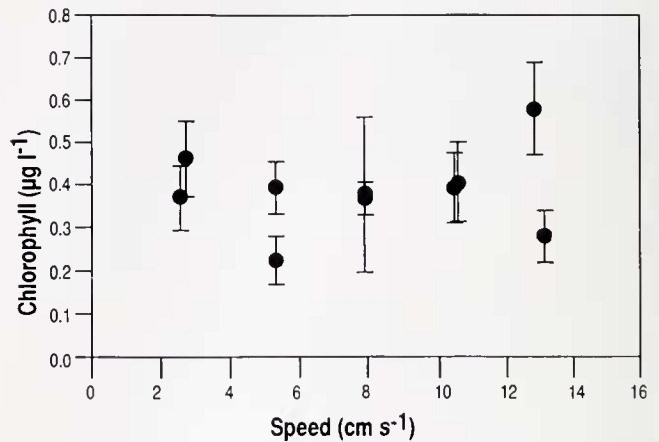


Figure 7. Concentrations of chlorophyll as a function of flow speed in 1992. Other interpretations as in Figure 2. There was no significant best-fit regression.

Therefore, the horizontal flux of chlorophyll varied by a factor of only about 5 over the $5 \times$ range of flow speeds.

Growth rates of *Semibalanus cariosus* did not depend on flow speed (Fig. 8). The monotonic regression was not significant (for all b : minimum $P = 0.17$, maximum $r^2 = 0.22$), nor was the polynomial regression.

Growth rates of *Pollicipes polymerus* also did not depend on flow speed (Fig. 9). The monotonic regression was not significant (for all b : minimum $P = 0.38$, maximum $r^2 = 0.10$), nor was the polynomial regression.

Growth rates of *Balanus crenatus* appeared to be minimal at the two lowest flow speeds, to increase sharply to a maximum growth rate at $U \approx 8 \text{ cm s}^{-1}$, and to decline

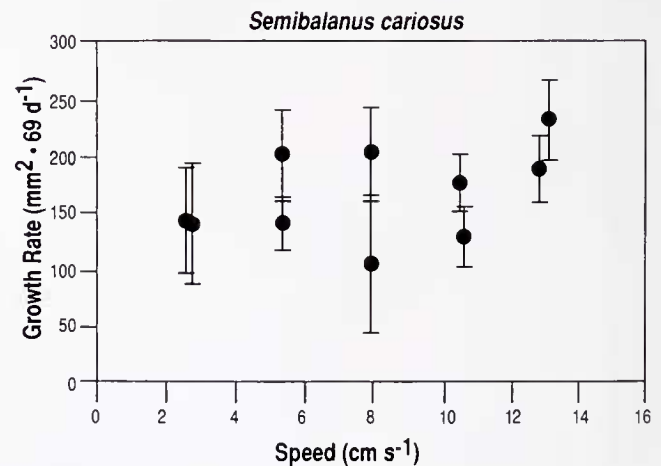


Figure 8. Growth rates of *Semibalanus cariosus* as a function of flow speed during the 69-day deployment in 1992. Other interpretations as in Figure 4. There was no significant best-fit regression.

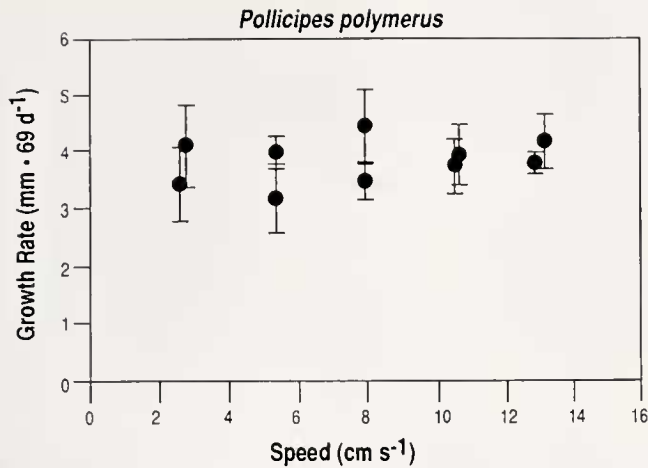


Figure 9. Growth rates of *Pollicipes polymerus* as a function of flow speed during the 69-day deployment in 1992. Other interpretations as in Figure 4. There was no significant best-fit regression.

at higher speeds (Fig. 10). Polynomial regression indicates that this convex-upward trend was weak and not significant at the conventional level of $P = 0.05$ ($r^2 = 0.49$, $P = 0.09$). However, further evidence of a speed-dependent growth response is supported by results of ANOVA, which indicated that replicate pipe effects were not significant ($F_{5,60} = 0.63$, $P = 0.68$), but that effects of flow level on growth were highly significant ($F_{4,65} = 3.66$, $P = 0.0095$). *A posteriori* multiple comparison tests (T-method—Sokal and Rohlf, 1981, p. 246) indicated that growth rates at $U = 8 \text{ cm s}^{-1}$ significantly exceeded those at $U = 2.7$ and 5.3 cm s^{-1} ($\alpha = 0.05$).

Flume observations of feeding behavior

A detailed description of feeding behaviors as a function of flow speed is given in Table IV. The three balanoid barnacles (*Balanus glandula*, *Semibalanus cariosus*, and *B. crenatus*) all were able to control the cirrus (*i.e.*, actively sweep or hold the cirrus still and erect) over the entire range of flow speeds examined, with little or no deformation of the cirrus by flow. This similarity held despite the wide range of habitats in which these species typically occur. *Balanus glandula* and *S. cariosus* are found in moderate to comparatively high-energy intertidal regions in the Pacific Northwest. These species typically experience oscillatory flows that often have instantaneous speeds far higher than those examined in this study. In contrast, *B. crenatus* lives predominantly in relatively low-energy, subtidal environments. It more typically experiences tidal flows that are not often impacted by wind-generated surface waves. Although tidal currents in the region of the

Friday Harbor Laboratories can be quite strong (Eckman *et al.*, 1989), this species also thrives in areas of comparatively weak flow energy. Animals used in this study were collected from a quiescent environment where even free-stream flows typically are $<10 \text{ cm s}^{-1}$ (personal observations).

In contrast to the balanoid barnacles, the pedunculate barnacle *Pollicipes polymerus* never swept the cirral net through the water. This species curled the cirrus inward when exposed to stronger flows (a behavior and not a passive deflection of the cirrus by flow) and retracted the cirrus completely at the highest speeds examined. This dissimilarity from the balanoid barnacles held despite the fact that *P. polymerus* lives sympatrically with *S. cariosus* in comparatively high-energy intertidal regions.

The bryozoan *Membranipora membranacea* was able to extend and use the lophophore at flow speeds $\leq 10 \text{ cm s}^{-1}$. However, in the face of stronger flows, the lophophore bent and shook noticeably, and was retracted upon contact with moving particles. At the highest speed examined, tentacles were not able to open from the lophophore. *M. membranacea* typically encrusts thalli of kelps. It lives both on the surface-canopy species *Nereocystis luetkeana* and on several understory species whose thalli extend only tens of centimeters above the bottom. Although abundant on plants in high-current regions (personal observations), these essentially flat colonies are submerged deep in the boundary layer that develops on a thallus that typically is aligned somewhat parallel to flow direction. Thus even in high-flow regions, *M. membranacea* on thalli of surface-canopy plants would experience significantly lower flow speeds.

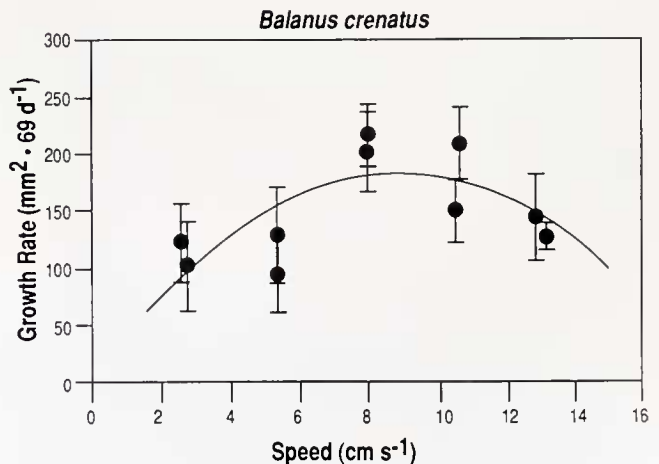


Figure 10. Growth rates of *Balanus crenatus* as a function of flow speed during the 69-day deployment in 1992. Other interpretations as in Figure 4. Also shown is the best-fit, 2nd-degree polynomial regression line obtained using the 10 mean values.

Table IV

Summary of feeding behaviors as a function of flow speed

Flow speed (cm s ⁻¹)	<i>Balanus glandula</i>	<i>Pollicipes polymerus</i>	<i>Semibalanus cariosus</i>	<i>Balanus crenatus</i>	<i>Membranipora membranacea</i>
2-3	Cirri of all animals sweep continuously (≈ 2 Hz)	(N.O.)	(N.O.)	(N.O.)	Lophophores extended; no deformation of tentacles by flow
4.5-6	Most animals sweep continuously; $\approx 10\%$ pause between sweeps to hold cirrus erect and still for ≈ 1 s	Cirri of all animals held erect and still; no deformation of cirral net	Cirri of all animals sweeping; cirrus retracts fully into mantle with each beat	Cirri of most animals sweeping; no cirral deformation by flow; rotation of cirrus up to 90° into flow is common	Lophophores extended; some weak shaking of tentacles by flow
8-10	Continuous sweeping predominates; $\approx 20\%$ pause briefly between sweeps	Cirri held erect and still; distal portions curled inward slightly (apparently by muscular action)	Many animals pause between sweeps to hold cirrus erect and still for 2-4 s; some animals rotate cirrus up to 90° to orient it into flow	As at 4.5-6 cm s ⁻¹	As at 4.5-6 cm s ⁻¹
14-18	$\approx 50\%$ sweep constantly; $\approx 50\%$ pause briefly between sweeps; no deformation of cirral net	Increased inward curl of cirri	Most animals pause between sweeps; cirral net not deformed by flow; rotation of cirrus up to 90° into flow is common	As at 4.5-6 cm s ⁻¹	Pronounced bending of tentacles in flow; lophophore retracts on contact with particles in transport
19-21	Most animals pause between sweeps; no deformation of cirral net	(N.O.)	(N.O.)	(N.O.)	Lophophores bent up to 45°
≥ 25	(N.O.)	Cirri almost totally retracted	As at 14-18 cm s ⁻¹	As at 4.5-6 cm s ⁻¹ , but some deflection of cirrus by flow at peak of extension	Tentacles unable to open from lophophore

(N.O.) = Not Observed at this speed.

The behavior of *Pseudochitinoipoma occidentalis* was not observed in flow. This species typically lives in cryptic, subtidal habitats such as the crevices in rocks and the undersides of rock ledges. Consequently, animals of this species normally would experience comparatively slow flow speeds.

Discussion

Results from the 1991 experiment provide clear evidence that growth rates of *Membranipora* and *Pseudochitinoipoma* declined significantly with increasing flow speed. In contrast, over the same range of flow speeds, there was no detectable relationship between speed and growth of *Balanus glandula*, though there was qualitative evidence of a weak inverse relationship. Higher growth rates of the bryozoan and serpulid occurred at weaker flows despite evidence that concentrations of suspended particulate

food may have been lower under these conditions (Figs. 2, 3). By the end of the 1991 experiment, we noted a substantial amount of material deposited on the bottoms of the pipes with weaker flows. Therefore, it is probable that the reduction in concentrations of suspended particles observed twice in the slowest flow pipes was consistent over time, and was caused by gravitational settlement of particles onto the bottom of a pipe, rather than removal of suspended particles by the small number of suspension feeders in each pipe. It is important to recognize that data presented in Figures 2 and 3 may overestimate differences among pipes in concentrations of food available to suspension feeders. Concentrations reported here characterized water exiting the ends of pipes, and gravitational settling would have produced less marked differences approximately halfway down the pipes, where animals were located. However, some differences would have occurred, and growth rates of the bryozoan and serpulid apparently

were greatest under low-flow conditions where food concentrations were also lowest. Had concentrations of suspended food been constant among treatments, we might have seen even stronger effects of flow on growth of these two species.

The 1992 experiment was prompted by the observation that growth of *Balanus glandula* was comparatively insensitive to flow speed, over a moderate range, in contrast to the pronounced sensitivities shown by the bryozoan and serpulid. More specifically, we were interested in determining the extent to which this difference related to the barnacle's behavior, its adaptation to a typically more energetic habitat, and its mechanical and morphological design. Regarding the latter, it seemed possible that barnacles might be generally more capable of feeding efficiently and growing well in a wider range of flows because the cirral net is composed of a rigid exoskeleton operated by a network of internal muscles (though each cirrus is extended hydraulically), and because they use the smaller (1st and 2nd) cirri to handle and process captured particles. These properties distinguish barnacles from many other suspension-feeding invertebrates, like the bryozoan and serpulid, that utilize feeding structures composed of soft tissue, that operate feeding structures mainly hydrostatically, and that process particles adhering to feeding structures primarily using cilia. These properties may render feeding more susceptible to fluid drag forces.

Combined results of the 1991 and 1992 experiments indicate significant differences in growth responses among barnacle species. There was no taxon-wide insensitivity of barnacle growth to flow speed, over even a moderate range of speeds. The interspecific variability relates most obviously to the range of flows that animals typically experience. Barnacles that inhabit comparatively high-energy intertidal environments (*Balanus glandula*, *Semibalanus cariosus*, and *Pollicipes polymerus*) grew well at a wide range of flow speeds (Figs. 5, 8, and 9). In contrast, growth rates of *B. crenatus*, which typically inhabits lower energy, subtidal environments, were significantly affected by flow speed and appeared to be maximal at a fairly weak, intermediate speed (about 8 cm s^{-1} ; Fig. 10). This pattern extends beyond the four species of barnacles studied. The bryozoan and serpulid, whose growth rates were lowest in the strongest flows (Figs. 4, 6), also typically inhabit subtidal microhabitats characterized by weaker flow (see above).

The interspecific variability in growth responses among barnacles was not obviously related to feeding behavior. Like the other balanoid barnacles, *Balanus crenatus* was apparently able to sweep with its cirrus over a wide range of flow speeds (Table IV), yet its growth—but not that of the others—was highly sensitive to flow speed.

We therefore conclude that, for each of the six species studied here, growth responses to flow speed were most clearly coupled to the relative flow energy of the animals' natural habitat. Growth response to flow did not reflect the clear similarities in morphology and behavior among some species. The mechanism(s) responsible for the observed differences among species are not obvious from our observations, and warrant further consideration.

Shimeta and Jumars (1991) extended the work of Rubenstein and Koehl (1977) to predict how features of a suspension-feeder's environment and structural aspects of its filtration apparatus combine to determine rates of particle contact with the filter. Their analysis indicates that rates of particle contact with an individual filter element should increase both with flow speed and with the concentration of food particles in suspension. In our experiments, flow speeds increased about $7.5 \times$, while food concentrations either remained constant (1992 experiment, Fig. 7) or simultaneously increased by about $2 \times$ (1991 experiment, Figs. 2, 3). Thus, rates of particle contact with an individual filter element should have increased with speed. Despite this prediction, we observed no monotonic increase in growth rate with increasing flow speed for any of the six species studied, and for two species (*Membranipora membranacea*, *Pseudochitinopoma occidentalis*) we noted an inverse relationship. The most reasonable explanation for this apparent contradiction is that, at speeds studied here, growth rates were governed by a strong inverse relationship between flow speed and efficiency at which particles are retained on the filter apparatus and passed to the point of ingestion. Among these species, the particle-handling abilities of the bryozoan and the serpulid were apparently more sensitive to speed than were those of *B. glandula*, *S. cariosus*, and *P. polymerus*. This heightened sensitivity of particle processing to flow may relate to the way that bryozoans and serpulids use cilia to process particles. An additional factor that may have contributed to the poor growth of the bryozoan and the serpulid in stronger flow is that their feeding apparatus (composed of soft tissue) may have experienced greater deformation in flows than the cirral nets of the barnacles (*cf.*, Patterson, 1984; Harvell and LaBarbera, 1985; Best, 1988; Shimeta and Jumars, 1991; Sponaugle and LaBarbera, 1991).

Some results from our growth study are consistent with many results from prior, shorter term studies that examined effects of flow on particle capture by "tentaculate" suspension feeders (Okamura, 1984, 1985; McFadden, 1986; Best, 1988; Leonard *et al.*, 1988; Sponaugle and LaBarbera, 1991). These studies all noted a maximum feeding rate at a low speed (though not necessarily at the lowest examined) and a strong decline in feeding rate at higher speeds. Our results confirm that at least two other

tentaculate suspension feeders (*M. membranacea* and *P. occidentalis*), and one species of barnacle (*B. crenatus*), exhibit a similar negative performance in strong flows, and that relationships noted previously between flow and particle capture probably translate into similar effects on somatic growth (see also Okamura, 1992).

In contrast to results of many previous studies of particle capture, for five of the six species studied we noted no reduction in growth rate at the lowest flow speeds (*i.e.*, no intermediate speed associated with a seemingly maximal growth rate). We suspect that this difference between our current and many previous results may in part reflect our experimental apparatus and design. The minimum flow speed examined was about 2 cm s^{-1} , and our pipe flows were all turbulent. In the absence of flows strong enough to interfere with particle processing, the supply of food to animals at 2 cm s^{-1} may have been high enough to ensure maximum growth rates. Moreover, the comparatively efficient mixing of particles in turbulent flows may have prevented an animal's feeding ambit from becoming depleted of food, even at the lowest flow speed. Had we included a flow speed slow enough to establish laminar, and not turbulent, conditions in a pipe, a marked reduction in growth rate might have resulted. At least two of the species studied here (*M. membranacea* and *P. occidentalis*) have no obvious mechanism for avoiding re-filtration of water already depleted of particles in extremely weak flows. A reduction in growth rates of *M. membranacea* was noted when colonies were exposed to laminar flows at speeds $< 0.5 \text{ cm s}^{-1}$ (Grunbaum, 1992).

Our results help to confirm a conclusion we have drawn previously (Eckman and Duggins, 1991) about the factors that affect growth of *Pseudochitinopoma occidentalis* *in situ*. This serpulid grew faster in weaker flows found beneath canopies of understory kelps than within more energetic clearings in the canopy. Results of our manipulative experiments implicated flow as one of several factors responsible for this pattern. Our current results confirm that this species of tentaculate suspension feeder is poorly adapted for life in stronger flow environments.

In conclusion, we have shown that there is wide variability among six species of benthic suspension feeder in the sensitivity of growth rate to a fixed range of comparatively moderate flow speeds between about 2 and about 15 cm s^{-1} . The growth response of animals to flow related most obviously to the range of flows typically experienced by the animal. Animals that inhabited comparatively weak flow environments showed a strong sensitivity to flow speed, whereas animals from comparatively high-energy environments were relatively insensitive to flow speed. Growth responses to flow did not reflect the clear similarities in morphology and behavior

among some species. We suspect that a key to understanding the impact of flow on a suspension feeder's growth is the animal's ability to handle and process particles that have impacted the feeding structure, and to deliver them to the point of ingestion. Further study of this phenomenon may significantly increase our understanding of the influence of hydrodynamic processes on benthic suspension feeders.

Acknowledgments

The considerable efforts of Amy Sewell were instrumental in the completion of this research. Helpful comments on earlier versions of the manuscript were provided by Drs. Carl André, Drew Harvell, Roberta Marinelli, and Don Webb, and by an anonymous reviewer. Dr. Dan Grunbaum assisted with observations on the feeding behavior of *Membranipora* in flow. Dr. Jon Grant provided access to the CHN analyzer at Dalhousie University. Figures were prepared by Anna Boyette and Suzanne McIntosh. We thank A.O.D. Willows, Director of the Friday Harbor Laboratories, and the staff of the Labs for their critical support and assistance. We also thank the Department of Oceanography at Dalhousie University for providing office space for one of us (JEE) during a sabbatical leave. This research was supported by NSF grant OCE-8911116.

Literature Cited

- Best, B. A. 1988. Passive suspension feeding in a sea pen: effects of ambient flow on volume flow rate and filtering efficiency. *Biol. Bull.* 175: 332-342.
- Eckman, J. E., and D. O. Duggins. 1991. Life and death beneath macrophyte canopies: effects of understory kelps on growth rates and survival of marine, benthic suspension feeders. *Oecologia (Berl.)* 87: 473-487.
- Eckman, J. E., C. H. Peterson, and J. A. Cahalan. 1989. Effects of flow speed, turbulence, and orientation on growth of juvenile bay scallops *Argopecten irradians concentricus* (Say). *J. Exp. Mar. Biol. Ecol.* 132: 123-140.
- Ellison, A. M., and C. D. Harvell. 1989. Size hierarchies in *Membranipora membranacea*: Do colonial animals follow the same rules as plants? *Oikos* 55: 349-355.
- Fréchette, M., and E. Bourget. 1985. Food-limited growth of *Mytilus edulis* (L.) in relation to the benthic boundary layer. *Can. J. Fish. Aquat. Sci.* 42: 1166-1170.
- Fréchette, M., C. A. Butman, and W. R. Geyer. 1989. The importance of boundary-layer flows in supplying phytoplankton to the benthic suspension feeder, *Mytilus edulis* L. *Limnol. Oceanogr.* 34: 19-36.
- Grunbaum, D. 1992. Local processes and global patterns: Biomathematical models of bryozoan feeding currents and density dependent aggregations in Antarctic krill. Ph.D. Thesis, Cornell University.
- Harvell, C. D., and M. LaBarbera. 1985. Flexibility: A mechanism for control of local velocities in hydroid colonies. *Biol. Bull.* 168: 312-320.
- Harvell, C. D., H. Caswell, and P. Simpson. 1990. Density effects in a colonial monoculture: experimental studies with a marine bryozoan (*Membranipora membranacea*). *Oecologia (Berl.)* 82: 227-237.

- Kirby-Smith, W. W. 1972. Growth of the bay scallop: the influence of experimental water currents. *J. Exp. Mar. Biol. Ecol.* **8**: 7-18.
- Leonard, A. B., J. R. Strickler, and N. D. Holland. 1988. Effects of current speed on filtration during suspension feeding in *Oligometra serripinna* (Echinodermata: Crinoidea). *Mar. Biol.* **97**: 111-126.
- McFadden, C. S. 1986. Colony fission increases particle capture rates of a soft coral: advantages of being a small colony. *J. Exp. Mar. Biol. Ecol.* **103**: 1-20.
- Okamura, B. 1984. The effects of ambient flow velocity, colony size, and upstream colonies on the feeding success of bryozoa. I. *Bugula stolonifera* Ryland, an arborescent species. *J. Exp. Mar. Biol. Ecol.* **83**: 179-193.
- Okamura, B. 1985. The effects of ambient flow velocity, colony size, and upstream colonies on the feeding success of bryozoa. II. *Conopeum reticulum* (Linnaeus), an encrusting species. *J. Exp. Mar. Biol. Ecol.* **89**: 69-80.
- Okamura, B. 1987. Particle size and flow velocity induce an inferred switch in bryozoan suspension-feeding behavior. *Biol. Bull.* **173**: 222-229.
- Okamura, B. 1992. Microhabitat variation and patterns of colony growth and feeding in a marine bryozoan. *Ecology* **73**: 1502-1513.
- Parsons, T. R., Y. Maita, and L. M. Lalli. 1984. *A Manual of Chemical and Biological Methods for Seawater Analysis*. Pergamon Press, New York.
- Patterson, M. R. 1984. Patterns of whole colony prey capture in the octocoral, *Alcyonium siderium*. *Biol. Bull.* **167**: 613-629.
- Patterson, M. R. 1991. The effects of flow on polyp-level prey capture in an octocoral, *Alcyonium siderium*. *Biol. Bull.* **180**: 93-102.
- Rubenstein, D. I., and M. A. R. Koehl. 1977. The mechanisms of filter feeding: some theoretical considerations. *Amer. Natur.* **111**: 981-994.
- Schlichting, H. 1979. *Boundary-Layer Theory*, 7th ed., McGraw-Hill Book Co., New York. 817 pp.
- Sebens, K. P., and A. S. Johnson. 1991. Effects of water movement on prey capture and distribution of reef corals. *Hydrobiol.* **226**: 91-101.
- Shimeta, J., and P. A. Jumars. 1991. Physical mechanisms and rates of particle capture by suspension feeders. *Oceanogr. Mar. Biol. Annu. Rev.* **29**: 191-257.
- Smith, F. G. W. 1946. Effect of water currents upon the attachment and growth of barnacles. *Biol. Bull.* **90**: 51-70.
- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry*, 2nd ed., W.H. Freeman & Co., San Francisco. 859 pp.
- Sponaugle, S., and M. LaBarbera. 1991. Drag-induced deformation: a functional feeding strategy in two species of gorgonians. *J. Exp. Mar. Biol. Ecol.* **148**: 121-134.
- Vogel, S. 1981. *Life in Moving Fluids*. Princeton University Press, Princeton, NJ. 352 pp.
- Vogel, S., and M. LaBarbera. 1978. Simple flow tanks for research and teaching. *Bioscience* **28**: 638-643.
- Wildish, D. J., and D. D. Kristmanson. 1979. Tidal energy and sublittoral macrobenthic animals in estuaries. *J. Fish. Res. Board Can.* **36**: 1197-1206.
- Wildish, D. J., and A. M. Saulnier. 1992. The effect of velocity and flow direction on the growth of juvenile and adult giant scallops. *J. Exp. Mar. Biol. Ecol.* **133**: 133-143.
- Wildish, D. J., D. D. Kristmanson, R. L. Hoar, A. M. DeCoste, S. D. McCormick, and A. W. White. 1987. Giant scallop feeding and growth responses to flow. *J. Exp. Mar. Biol. Ecol.* **113**: 207-220.